Comparative Breeding Site Ecology and the Adaptive Radiation of Picture-Winged Drosophila (Diptera: Drosophilidae) in Hawaii[1]

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One of the more prominent concerns in biology is the explanation of the adaptation and speciation expressed in the diversity of living things. Many observers have turned to the life of islands, believing that processes could be seen in microcosm, where at least in a relative way, patterns would be simpler. It follows that the most isolated island group, the Hawaiian Archipelago, would best merit attention. Charles Darwin recognized this in the middle of the last century, noting that each island of the Hawaiian group was well isolated from the other. He wrote that he "would subscribe 50£ to any collector to go there and work. . . ." (Francis Darwin, 1903).

In Hawaii, the most fruitful subjects for study would be a large and extensively differentiated complex of organisms with features that permit several analytical approaches. All of these characteristics are found in the approximately 750 species of native Drosophilidae (Perkins, 1913; Zimmerman, 1958; Hardy, 1965).

These tenets were realized in 1961 by D. Elmo Hardy and Wilson S. Stone of the University of Hawaii and the University of Texas respectively, when they jointly launched a multidisciplinary investigation of the drosophilid fauna of the Hawaiian Islands. It can be said that their efforts have been well rewarded (Carson, Hardy, Spieth, and Stone, 1970; Robertson, 1970; and the reviews of Clarke, 1970; and Stainer, 1971). However, some of the work on the picture-winged group of flies (110 described species) was frustrated since without information on the natural oviposition substrates, a number of species could not be induced to oviposit on laboratory media. Even with host knowledge, some species did not oviposit in culture. *Drosophila substenoptera* and *D. turbata* are two such examples in which the salivary gland chromosomes could be studied only from field collected larvae. A sizable number of other species were known from very few or single specimens, their extreme rarity prompting speculation that they were close to extinction. Essentially, the picture-winged group, containing the very species that had been extensively scrutinized in most aspects, was little understood in relation to oviposition and larval feeding sites, which are basic elements of their bionomics.

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Recognizing the utility of host information, Carson (1971) wrote: "The time now appears ripe to exploit the knowledge of breeding sites for an understanding of the genetic events which occur in natural populations and which are responsible for changes leading to adaptation and speciation."

In this paper I will present numerous new data on the nutrition sources of picture-winged *Drosophila* larvae. This information is then organized into tables showing distinctive patterns of host plant preference in these flies. These patterns are correlated to published information establishing cytological subgroups based upon chromosomal morphology. Finally, the role of host selection behavior in the adaptive radiation of the picture-winged *Drosophila* will be discussed.

Literature Review

Some early entomologists recognized that the Drosophilidae of Hawaii were a quite remarkable component of the insect fauna, but Perkins (1906, 1910) provided only a general account of their breeding sites, mentioning specifically only lobeliads and *Pisonia*. Perkins was sent to Hawaii from 1892-1897 by the British Association for the Advancement of Science to conduct a survey of the land fauna during which time he noted the study left to be done, then wrote: "The minute and obscure Diptera, consisting largely of small Dolicopodidae and the infinite numbers of Drosophilidae have been little collected" (Perkins, 1902). Otto Swezey (1952, 1954) carefully reared many hundreds of species of insects from native trees, shrubs and plants, but gave minor attention to *Drosophila* during his fifty years of insect study. Hedrick and Burke (1950, 1951) published a brief report on yeasts from larvae sent to them by Gordon Mainland, but the plant hosts for these specimens apparently have not been published.

With the appearance of D. E. Hardy's voluminous monograph on the indigenous members of the family in 1965, intensive evolutionary and ecological studies were feasible. W. B. Heed (1968) soon published detailed records of drosophilids of most subgroups, particularly those breeding in rotting leaves of *Cheirodendron*. Because of this emphasis upon leaves, few of the picture-winged species were obtained in his rearings. Kircher (1969) followed with a biochemical analysis of the *Cheirodendron* leaf and Kambysellis and Heed (1969) correlated ecology with ovarian structure and function. Then, Heed (1971) presented an overview of existing ecological information. Robertson et al. (1968) attempted to apply this ecological knowledge to the laboratory culture of leaf-breeding *Drosophila*. Kaneshiro et al. (1973) described an especially elegant case of breeding niche separation. Recently, Heed (in preparation) made a detailed comparative study of the drosophilids inhabiting several climatically and floristically differing kipukas.

Through a coordinated research program on the Hawaiian *Drosophila*,

there is now a great deal of information about many aspects of their biology. Hardy and Kaneshiro (1968, 1969, 1971, 1972) provided names as new picture-winged species were discovered. Wheeler and Clayton (1965) succeeded in establishing many laboratory cultures. Spieth (1966, 1968) produced outstanding studies on mating behavior and Throckmorton (1966, and in preparation) on internal anatomy and phylogeny. Carson and Stalker (1968, 1969) and Clayton, Carson and Sato (1972) published a remarkable set of polytene chromosome inversion analyses from which they have constructed a master diagram of interspecific relationships. This diagram, now including about 100 species, offers unique opportunities to correlate host plant selection and other ecological data to precise information on relationships based upon chromosomal morphology. The extensive new genetic information is now contributing greatly to a better understanding of speciation (Carson, 1971 and Dobzanshky, 1970).

The methods employed in the present study follow in many respects those of Heed (1968), in which larvae within natural substrate materials were discovered, brought to the laboratory, and reared to maturity so that identifications could be made and voucher specimens obtained. A new and effective technique was the extensive application of plant ecological and taxonomic knowledge to the search for new host plant species and breeding sites in the native flora. The basic literature for this was the plant distributional information of Rock (1913), Degener and Degener (1935-1972) and Hillebrand (1888).

Materials and Methods

On each of the six larger islands, districts with wet, moist and dry climates and with predominantly native vegetation were surveyed for breeding sites. Since the Drosophilidae, with few exceptions, are specialized for a phyto-saprophagous habit, dying and decomposing plant parts, particularly rotting bark and fermenting sap exudates, were sought and examined for eggs and larvae. Heed (1968 and in preparation) has searched rotting leaves extensively for the presence of larvae, and found them to harbor large numbers of species, but only a few from the picture-winged group. Thus a detailed examination of sap fluxes, soft wood and bark was made. A long, sturdy knife was used in prying loose bark that was only slightly softened by decay processes. A small foldable saw, and sometimes a chisel, were used on the hard-wooded trees with sap fluxes since larvae often were deep in crevices.

Plastic bags labeled with freezer tape or paper cards were used to retain both the moisture and larvae and to limit mold contamination during transit. Ventilation was provided by folding the plastic bag very loosely. It could then be placed in an organdy bag which was tied if the larvae were active. Transportation to the laboratory is a critical stage because the native *Drosophila* are sensitive to heat, sunlight, abrasion,

and desiccation during transit. Thus, ice chests were used to carry the substrate materials from the field at temperatures of 50°-60°F.

Larvae and substrate were placed on two inches of moist sand in a labeled jar or can, then covered with a flexible polyethylene sheet closely fastened with a rubber band. Vents in the cover were kept plugged with cotton except during aspiration of adults. The containers with larvae were held at a controlled temperature of 68°-70°F.

Adults began emerging from the sand in two weeks to six months, depending upon the species, nutritional content of the substrate, temperature and crowding. The usual period was four to eight weeks, but some larvae, especially in *Tetraplasandra* bark, required as long as 16 weeks. Adults were fed on Wheeler-Clayton medium for 10 days, then some were cultured and the rest were sacrificed, pinned and labeled. Identifications were checked by K. Y. Kaneshiro.

Results and Discussion

Appendix 1 lists the complete records of 81 species of endemic, picture-winged *Drosophila* (plus an additional very unusual species, *D. quasianomalipes*) for which host plant information is now known. The records of Heed (1968) for 11 species have been included. A separate section (Sec. C) of the appendix with rearing records for five members of the family exotic to the Hawaiian Islands is provided, since these sometimes occur in the same sites as native species.

Collection code numbers are listed in Appendix 1 to facilitate future reference to field notes and culture stocks. A great many collectors have assisted the author to varying degrees, and these are noted at the end of the appendix.

Tables 1-7 assimilate and condense the data contained in Appendix 1. Included are data on 56 host-plant species from which over 3300 specimens of picture-winged flies have been reared. The seven tables have been delimited so that the host plants are grouped to most clearly reflect patterns of use by the flies. In most cases these patterns coincide with botanical taxa, usually at the family and order levels. The vertical columns illustrate the presently known drosophilid usage of the host plants on each of the main islands. Oahu has received much greater attention than other islands in this study because it is accessible without interisland transportation. The number of entries in the "Oahu" column of Tables 1-8 are consequently much more numerous and may allow clearer discernment of ecological phenomena. A complete list of the host plants (Table 11) is arranged phylogenetically, according to Cronquist (1968).

The blank space on Table 1 under Maui Island for the *Reynoldsia* indicates that a search for larvae in this plant is needed. Likewise, future collections on the Island of Kauai on the host plants *Charpentiera, Freycinetia,* and *Sapindus oahuensis* can be expected to produce new host records and some new species of *Drosophila*. This situation is sim-

ilar to that found in *Lobelia* by Hedberg (1958) on African alpine areas. Each mountaintop usually harbored a distinct but related *Lobelia* that he termed vicarious or cognate species.

There is a single record of an *adiastola* subgroup species, *setosimentum,* having been reared from *Cheirodendron* bark, and a record of one species of subgroup IV, *punalua,* having been reared from *Tetraplasandra.* These exceptional cases, involving only a tiny fraction of the specimens reared, are highly instructive because they further reinforce the hypothesis that Araliaceae were the breeding substrates for Hawaii's ancestral drosophilids. Even though these two flies specialize upon Lobeliaceae and *Freycinetia,* respectively, a remnant of an affinity for the Araliaceae persists. This probably results from a lower threshold in the females for acceptance of Araliaceae as an oviposition substrate.

Another case where host preference links the Araliaceae with a derived host has been found in *D. ciliaticrus.* The first two records indicated this fly to be highly specific to *Dracaena* (Liliaceae), but subsequent data showed it to be equally attached to two more plants in the lowland and midland environment, *Reynoldsia* and *Tetraplasandra hawaiiensis* (Araliaceae).

An analogous situation is found among the 400 species of *Papilio* butterflies, very many of which feed on Rutaceous host plants (Dethier 1941), while a small number of species are, to quote Dethier, "rabidly addicted" to Umbelliferae but on occasion do revert to Rutaceae. After a study of the essential oils, especially methyl chavicole and anethole, Dethier postulated a pathway by which the Umbelliferae were relatively recently acquired as host plants. It may prove rewarding to gather information on essential oils of *Drosophila* host plants in Hawaii.

In 1969, Carson and Stalker reported that *Drosophila primaeva,* an unspecialized fly endemic to Kauai, possesses certain chromosomal segments in common with species of the predominantly Palearctic *robusta* group, thereby placing it at the base of the chromosomal relationship diagram. On both occasions when *primaeva* has been reared, it was from Araliaceae bark. This suggests that the closest relatives of the Hawaiian *Drosophila* may be found breeding upon araliaceous substrates in the Indo-Pacific region.

Another "araliad fly", but not a picture-winged species, is *D. quasianomalipes.* It occupies a pivotal phylogenetic position according to Spieth (1970) because both drosophiloid and scaptomyzoid elements are present in its mating behavior. It should also be noted here that this species and *primaeva* are both endemic to Kauai, oldest of the present-day high islands and a center of diversity and abundance of the native Araliaceae.

The data are presently insufficient to establish whether host races are present in this fauna. Perhaps further work will help discriminate ecological races involving morphologically similar or indistinguishable allo-

trophic populations, each being restricted to a different host or group of hosts. The recent discovery that on Kauai and Oahu *grimshawi* is rare and breeds only in *Wikstroemia* bark, while on Maui, Molokai and especially Lanai the same species is abundant and breeds on a wide range of host plants, may indicate ecological race formation.

Host Selectivity. An examination of Table 10 reveals that of the 80 species listed, 62 (77%) of the total oviposit upon and develop within the rotting parts of plants belonging to a single family. These are termed monophagous species. Almost half of this group have been collected as larvae only once and the data seem inconclusive. However, the very reason so few rearings of these flies have been secured attests to the flies' rarity and narrow specialization, and also to the scarcity and localization of several hosts, such as *Touchardia, Sapindus,* and *Reynoldsia.* The definitions of the three levels of selectivity were based upon judgment derived from extensive field experience and hundreds of samples.

In contrast to the 62 monophagous *Drosophila* are the five polyphagous species (breeding in five or more host families) best typified by *D. crucigera* of which 327 specimens have been taken from 21 different plant families on 55 occasions. Notably, this species is adapted to the use of four host species exotic to Hawaii. *D. grimshawi,* another polyphagous species, has utilized the fruits of another exotic, *Solanum sodomeum.* Three additional species are polyphagous: *villosipedis, gradata,* and *hawaiiensis.* The latter two are ecologically distinguished in that they show a strong preference for sap exudates, as opposed to rotting bark or fruits.

The oligophagous flies (those which utilize two, three or four host families) are 17% of the total species. The number of oligophagous species is greatest on the youngest island of Hawaii (8) with far fewer on Maui (2), Oahu (4) and Kauai (1). Among the polyphagous species, no strong trend is evident: Hawaii (1), Maui (1), Oahu (2), and Kauai (2).

Host Associations Within Subgroups. Figure 1 represents graphically the use of 12 basic host plant genera by the four largest cytologically defined subgroupings of *Drosophila.* The plant genera are listed across the horizontal axis in the same sequence as in Tables 1-7, while the vertical axis indicates the number of species breeding in each host genus. The outstanding impression given is the wide range of hosts utilized by the *grimshawi* subgroup. These species have exploited all 12 genera of plants listed, and all of the five polyphagous species belong to this group.

There is a cluster of 18 *grimshawi* subgroup species, exemplified by *orphnopeza,* which have been reared only from Araliaceae bark and sap. Breeding in these same sites is another cluster of seven larger species belonging to the *planitibia* subgroup. The size differential between these two subgroups merits further analysis as it indicates character displacement.

Some *Drosophila* have been found to survive and reproduce below 600 ft, an elevation that previously was thought (Carson et al. 1970)

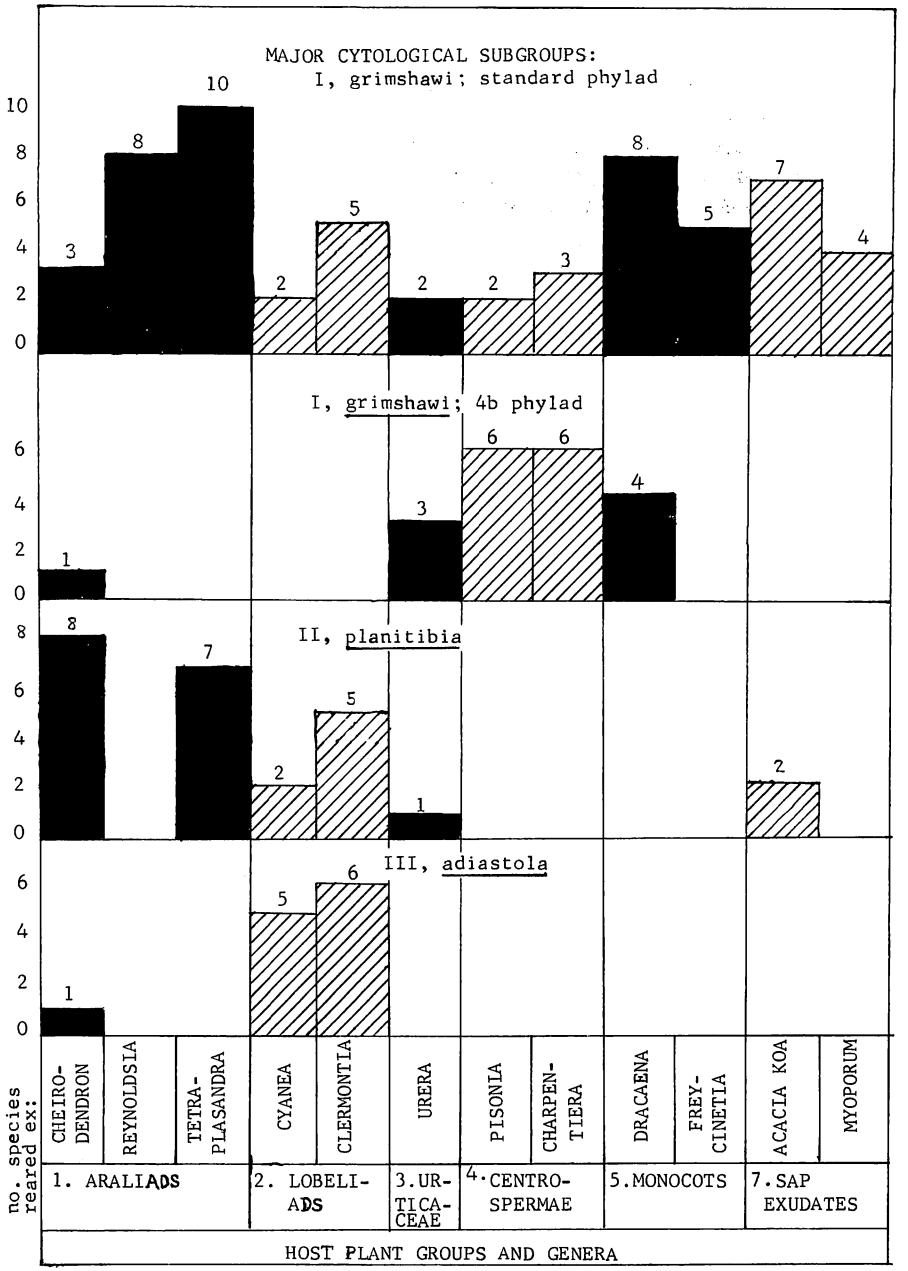

FIG. 1. Patterns of host plant usage by *Drosophila*.

to be the minimum inhabitable by native species. Significantly, all four of these flies *(grimshawi, ciliaticrus, hawaiiensis,* and *reynoldsiae)* are members of the opportunistic *grimshawi* subgroup. They breed in *Reynoldsia* stems, thereby taking advantage of what little substrate material is available in the xerophytic or dry forest, (about 25 in annual rainfall) as low as 300 ft or even 100 ft above sea level. They are not confined to this climatic region except *D. reynoldsiae* which, to use evolutionary terminology, has entered a new adaptive zone. Rather, the range of the first three species extends from the higher elevation mixed forests or rain forests.

A primary observation here is that native *Drosophila* almost always can be found wherever their native host plants occur. A striking example of this was the discovery of *reynoldsiae* at Kului Gulch in the Koolau Mountains. In this area only four host trees have been located among hundreds of acres of exotic *Schinus* and *Psidium.*

Figuratively, a second frontier has been crossed within the *grimshawi* subgroup and another new adaptive zone, sap exudates, has been extensively exploited by one quarter of its members. These breeding sites support 14 species of closely related picture-winged *Drosophila* which share chromosomal inversion 2b (Clayton et al., 1972). Two isolated exceptions, *picticornis* of the *planitibia* subgroup and *paucicilia* of the *punalua* subgroup have shifted separately to sap exudates in a parallel manner. The fermenting sap of five genera of trees *(Acacia, Myoporum, Sapindus, Osmanthus,* and *Myrsine)* has been used in this adaptive radiation of species in the 2b phylad. These flies are very successful and range widely. *D. silvarentis* occurs from elevations of 10,000 ft in areas of low rainfall to rain forests and mixed forests where its *Myoporum* and *Osmanthus* hosts also grow.

In all groups of host plants it is possible to classify breeding sites easily and clearly as being either rotting bark or fermenting sap exudate, but with one exception, the Araliaceae. There the distinctions blur enough that only the appellation "rotting bark and/or sap flux" or "bark-flux" is sufficiently descriptive of some substrates. Carson (1971) has reported a similar difficulty in differentiating between fluxing situations and necrosis of bark tissue in Salicaceae of North America. Cronquist (1968) has commented that the araliads have a well developed secretory system, the function of which has not been demonstrated. Hawaii's Araliaceae conform to this generalization by copiously giving a viscous sap in response to a break in the bark. Upon drying, it becomes gummy *(Tetraplasandra* and *Reynoldsia)* or brittle *(Cheirodendron).* This sap very possibly serves to frustrate attacks by cerambycid beetles, which are virtually absent in these plants, but the slow decay of the bark and sap provide ideal *Drosophila* larval sites.

Notably, the two species most often collected in "bark-flux", *gradata* and *hawaiiensis,* are also found in "bark" proper in araliads and "flux" proper in a wide array of plants. Although the data are scanty, they sug-

FIG. 2. The leeward East Maui dryland sclerophyll forest at Auwahi, where *Cheirodendron, Tetraplasandra, Reynoldsia, Dracaena, Osmanthus, Myoporum and Charpentiera* occur. Among these are the host plants for seven species of picture-winged *Drosophila*. Photo by Earl Bishop.

FIG. 3. *Cheirodendron platyphyllum* in the summit cloud forest of Wiliwilinui Ridge, East Oahu. *Drosophila substenoptera, D. oahuensis, D. nigribasis* and *D. pilimana* have been reared from the decaying bark of this tree. At lower left is a terminal stem of the climber, *Freycinetia arborea,* which hosts *D. punalua.* Photo by C. H. Lamoureux.

gest to me that the flux-breeding species arose from forms breeding in Araliaceae bark. I believe the magnitude of the adaptive shift was reduced in these species because adaptation to the araliaid bark-flux substrate preadapted them to a substrate consisting solely of sap exudate.

The shift may well have been made first from *Tetraplasandra* flux to *Sapindus* flux on Kauai or Oahu by the ancestors of the modern *flexipes*. This postulation is supported by Hegnauer's (1964) account of similarities in chemical constituents, such as abundant triterpenic saponins and acetylenic compounds, some of which may either influence the microflora of the flux or serve directly as oviposition cues for gravid female *Drosophila*. Because of chemical and morphological similarities, I have often used the term "araliads" to encompass both the Araliaceae and the somewhat closely related Sapindaceae. These host plants are of greatest importance to the non-picture-wings also: of the 176 species Heed (1968) reared, 35% were from araliads.

Figure 1 shows that only the araliad host group is utilized by all four cytological subgroups of picture-winged *Drosophila*. In addition, two subgroups not shown there, IV and V, make significant use of these hosts. Only the Lobeliaceae even remotely approach the araliads in total usage by the *Drosophila*.

Native Parasites of Drosophila. The levels of predation and parasitism are generally regarded to be comparatively low on oceanic islands, and Zimmerman (1948) concurs with this for Hawaii, adding that parasite pressures have not played a major role in insect species formation. During the present study only ten collections out of a total of over 300 yielded parasites. These produced 28 adult Eucoiline wasps, while in the same period 2,000 specimens of picture-winged *Drosophila* were reared, which appears to substantiate Zimmerman's position. However, on a few occasions, large numbers of field collected larvae have failed to mature under laboratory conditions. For example, from a large collection of *oahuensis* and *sobrina* larvae (identifications of parasitized larvae provided by H. L. Carson), no flies and only two wasps were reared. Possibly the parasites eliminate large numbers of their host, but then fail to complete their development under laboratory conditions. Parasitic wasps required a long period (60-90 days) before emerging. Specimens of an unusual, wingless diapriid wasp (*Platymiscoides* sp.) were reared from a single collection of *Drosophila* larvae in *Cheirodendron* bark.

On the other hand, Perkins (1913), who was a specialist on Hymenoptera, wrote that the larvae of *Drosophila* are very subject to the attacks of Hymenopterous parasites. He noted that *Proctotrypes hawaiiensis, Phaenopria* sp., *Spalangia lanaiensis* and Eucoiline wasps had been bred extensively from them. Zimmerman lists *Eucoila,* a genus of 9 species and *Cothonaspis,* which contains 18 species, as cynipid genera which include *Drosophila* parasites. Of the 9 Diapriidae then known to be native to Hawaii, he notes that several are *Drosophila* parasites. *Eupelmids* (54 spp.) are parasites of Diptera as well as the Lepidoptera and Coleoptera

FIG. 4. The *Metrosideros* rain forests of Hawaii have much ground cover and a mid-level canopy of tree ferns and such host plants as *Cheirodendron, Tetraplasandra, Clermontia* and other Lobeliaceae. Photo by D. Mueller-Dombois.

with which they have been more frequently associated. Timberlake (1924) recorded a *Drosophila* sp. parasitized by *Pachycrepoideus dubius* Ashmead (Pteromalidae). Swezey (1935) reports a figitid (Eucoilinae) wasp from puparia in *Freycinetia* fruit.

Heed (1968) wrote that hymenopterous parasites commonly are found emerging from the eaten out pupal cases of drosophilids. J. W. Beardsley has studied a series of 16 specimens reared by Heed in association with *Drosophila* from *Clermontia* bark collected at Waikamoi, Maui. These were determined to be *Hypodiranchis* sp., possibly *H. oblonga* Yoshimoto (Eucoilinae).

Native Predators of Drosophila. The literature citations of *Drosophila* predators are no more extensive than those for parasites. Crabronid wasps are known to provision nests with the larger *Drosophila,* Calliphoridae, Dolichopodidae and Anthomyiidae. Swezey (1918) took a female *Drosophila oahuensis* from a nest of *Ectemnius tumidoventris* (Perkins) and Bridwell (1919) found two "*Drosophila* or allied flies" among 300 tephritids in a nest cell of *Ectemnius nesiotes* (Pate). Perkins (1913) found that *E. tumidoventris* often fills its cells entirely with *Drosophila.*

Adult and larval *Lispocephala* (Diptera: Muscidae) are the most commonly encountered of the predators. Many species are large-sized flies, 10 mm or more in length, and are believed to be important predators of the drosophilids. Adults were collected while feeding, once on *D. setosimentum* and another occasion on a tipulid. *Lispocephala* adults were reared from 41 (13%) of the substrate collections, nearly always as single specimens, indicating they are cannibalistic. D. E. Hardy is currently working with this genus and estimates that there are at least 100 endemic species in Hawaii. He has determined that 13 species, most of which are undescribed, are represented among the 53 specimens reared along with *Drosophila* from a wide range of breeding sites. From the available information, it is not possible to comment with certainty on the degree of specificity of *Lispocephala* species to either breeding sites or to host *Drosophila* species, but it appears to be very low. As an example, of 14. *L. ingens,* four were reared from hosts in araliaid bark, seven from lobeliaids, two from *Pipturus* and one from a fungus. Thirty-two percent of all *Lispocephala* adults were retrieved from araliaid substrate material, and 40% from lobeliaid material. Not a single *Lispocephala* has been recovered from sap fluxes, but otherwise they have followed picture-winged *Drosophila* into the various host plant groups. It is common to find adults perched at *Drosophila* breeding sites, (probably being attracted by the fermentation odors) where they have been observed depositing their own eggs. My data support Spieth's statement in Carson et al. (1970) that the gathering of *Lispocephala* predators at *Drosophila* breeding-feeding sites was a prominent factor in the exceptional development of lek behavior and of increased size in the native Hawaiian *Drosophila.*

In the insular environment of Hawaii there has occurred quite a bizarre development of entomophagy: the evolution of mantis-like predatory behaviors in such an unlikely insect as a caterpillar. A geometrid larva was discovered feeding on a large, robust calliphorid fly on Hawaii in January, 1972 (Montgomery and Mull, in preparation). Subsequent laboratory observations confirmed that large flies were actually seized when moving near the posterior end of the poised caterpillar. The legs, especially the tarsal claws, are elongated and bear heavy spines so that when extended they form a basket with which the prey are enclosed by means of an instantaneous backward reach. Consumption of four picture-winged flies brought the larva to maturity, and the moth has been deter-

mined by E. C. Zimmerman (pers. comm.) as belonging to the genus *Eupithecia*. Subsequently, 250 more specimens have been collected without great effort on the islands of Maui, Molokai, Lanai, Kauai and Oahu, indicating a wider distribution and greater abundance of these larvae than at first surmised. *Drosophila*, especially males that take up stations on leaf surfaces, may be seized by these geometrid predators, but more field study of their diet is essential to determine their role.

The Dolichopodidae or long-legged flies are very common in the same habitats as *Drosophila*, where they perch upon stems and leaves and among the litter on the forest floor. This family is extensively developed in Hawaii, with 208 species now known (Hardy and Kohn, 1964; Tenorio, 1969) and until as recently as 1948, it surpassed the Drosophilidae in numbers of described species. This, along with their characteristically predaceous habits, both as larvae and adults, raises the question of their relations with *Drosophila*.

What little is known of the biology of the native Dolichopodidae is due to the careful and well-illustrated works of F. X. Williams (1933, 1938, 1939) which centered upon aquatic environments. In the latest paper, he presented an account of *Campsicnemus fumipennis* Parent, which he found common on tree trunks in the rain forest along Lulumahu Stream at 2000 ft on Oahu. Though a scant 4 mm in adult body length, it is among the largest of its genus. Because picture-winged *Drosophila* average 5 mm in body length, they would seem too large a prey, and in fact, Williams found the chief food to be small springtails (Collembola), which *C. fumipennis* would follow and catch on the run with its labella. Oldroyd (1964) has explained that only small-sized prey are taken since the victim must be at least partially engulfed within the labella. Within this spongy sac, small, soft-bodied insects are torn open with hard, sclerotized "teeth" coming from pseudo-tracheae. Besides springtails, *Dasyhelia* midges (Ceratopogonidae) and dead termites are known to serve as food for the adults.

The larvae are recorded to feed naturally on moth fly larvae (Psychodidae), and in the laboratory, Williams reared a single *C. fumipennis* from egg to adult on a *Psidium guajava* L. fruit infested with *Drosophila melanogaster*. Even though these observations are few, it can be concluded that larvae of *Campsicnemus* generally feed on small and weak prey, perhaps no more than 2 or 3 mm in length, and have little impact on the picture-winged *Drosophila*. Only six species of dolichopodids were reared from drosophilid substrates during this study. These were determined by J. M. Tenorio of the Bishop Museum. Moderate numbers, overwhelmingly of *C. fumipennis*, occurred in approximately 10% of the collections in every class of host plant materials, except the sap exudates. A similar-sized species, *C. flaviventer* Hardy and Kohn, was much less commonly obtained. In addition, four specimens of smaller (ca 2 mm long) *Campsicnemus* spp. were reared. These represent three apparently new species, along with a single *C. drymoscartes* Hardy and Kohn. None of the large,

FIG. 5. The slopes of the Waianae Mountains support a vast, richly diverse mesophytic forest, as well as a much smaller cloud forest and summit bog on 4000′ Mount Kaala (background). Twenty-nine species of picture-winged *Drosophila* occur on West Oahu. Photo by Wayne Gagné.

uncommon *Sigmatineurum* (6 mm) or *Paraliancalus* (8.5 mm) were reared.

In his studies, Heed (1968) has not implicated the dolichopodids as a limiting factor on populations of the smaller drosophilids, such as in the modified mouth-part, ciliated tarsus, and scaptomyzoid groups. In conclusion, the attractive speculation that Hawaii's large and varied fauna of predatory Dolichopodidae co-evolved with the Drosophilidae has not been substantiated.

Introduced Predators. The big-headed ant, *Pheidole megacephala* Fabr., has long been credited (Perkins, 1913) with having a devastating effect on the native insect fauna wherever it ranges. This includes all low and

FIG. 6. Two larvae of *Drosophila orthofascia* or its relatives exposed by cracking open the decaying bark of *Tetraplasandra hawaiiensis*. Photo by Rick Warschauer.

FIG. 7. Larvae of *Drosophila pullipes* on the matted, fibrous bark of *Wikstroemia* which were exposed by stripping it back. Photo by Glenn Yamashita.

sometimes medium elevations, except for the very dry districts such as Kokohead, Kaena, and Ewa, on Oahu. In these districts Swezey was excited to discover several undescribed endemic moths and beetles associated with the *Euphorbia* and *Myoporum* at just a few feet above sea level where *Pheidole* apparently could not become established.

The role of this exotic ant in limiting the distributions or the very existence of certain species of the native Drosophilidae is uncertain because no collections of these flies were made before this ant arrived in the Islands about a century ago. Two records of *Drosophila* breeding were obtained from very low elevations (100 ft and 300 ft) in dry areas during this study which can be compared with future collection attempts at very low but wet, ant-inhabited districts. *Dracaena aurea* Mann, *Tetraplasandra racemosum* Forbes and *Charpentiera densiflora* Sohmer from the Nonou (600 ft) and Hoolulu, NaPali (700 ft) areas of lowland Kauai offer opportunities for determining the status of the drosophilid fauna under such conditions. Brief field efforts in these sites have already shown that at least *D. villosipedis* and *D. crucigera* do occur there.

A certain *Metrosideros* tree at 1800 ft in a valley near Milolii, Kauai was inspected for nymphs of Cixiidae and larvae of *D. picticornis* in August 1970 and October 1972. On both occasions these insects were present, but on the second visit special note was taken of *Pheidole* ants just inches away from these two native species but apparently not preying on them. This indicates that the lowland drosophilid fauna may not have been as much decimated by exotic ants as has been generally believed.

Summary

The Hawaiian Islands support 750 endemic Drosophilidae that, since 1963, have been intensively studied with respect to their systematics, behavior, cytology, and ecology. Concentrated collecting of decaying stems and sap exudates of native trees and shrubs has resulted in knowledge of the breeding sites for 80 (60%) of the species in the picture-winged group of flies. Polyphagy is less prevalent than was previously believed; only 6% of the ecologically known species utilize five or more families of host plants, only 17% utilize two to four families, and the remaining 77% appear to be specific to a single host family. Seven basic groups of host plants are distinguished: araliads, lobeliads, Urticaceae, Centrospermae, monocots, incidental hosts, and sap exudate producing plants. The most important group is the araliads, which provide breeding sites for 37% of the species reared. For this reason, and because the most primitive known species, *D. primeava,* also uses this substrate, the araliads are implicated as being the breeding site from which Hawaii's drosophilids radiated.

Of the 32 other plant families, the Lobeliaceae are the most used, with 15% of the picture-winged species depending upon these plants. Much less used, and more recently accepted, are the sap exudates of six genera of native trees. A single possible case of ecological race formation

has been distinguished. Parasites are found to exert a low pressure on fly populations, with only 3% of the substrates yielding eucoline wasps. Predation by the muscid fly genus *Lispocephala* is extensive.

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TABLE 1.—Drosphila *Reared from Araliads*

Plant Host	KAUAI	OAHU	LANAI/MOLOKAI	MAUI	HAWAII	Total spp.
ARALIACEAE						
Cheirodendron sp.	*quasianomalipes* 10:3*	*pilimana* 1:1 *nigribasis* 7:4 *oahuensis* 52:2		*orthofascia* 1:1 *cyrtoloma* 1:1	*murphyi* 21:3 *sproati* 53:3 *paucipuncta* 19:1 *silvestris* 4:1 *heteroneura* 4:1 *setosifrons* 3:2 *setosimentum* 2:1 *murphyi* 1:1	
Bark:	*primaeva* 5:1	*substenoptera* 37:2	M: *neopicta* 1:1			15
Tetraplasandra		*gradata* 1:1 *sobrina* 45:1	L: *orthofascia* 32:1	*orthofascia* 26:3	sp. nr. *sobrina* 3:1	
Bark:	*villosipedis* 2:1	*atrimentum* 23:2 *crucigera* 18:3 *punalua* 2:1 *nigribasis* 3:2 *oahuensis* 14:4		*orphnopeza* 13:3 *grimshawi* 2:1 *melanocephala* 12:2 *cyrtoloma* 2:1	*ciliaticrus* 2:1	
Bark-Flux:	*primaeva* 9:1	*substenoptera* 2:1		*neopicta* 16:2 *orthofascia* 23:1	*setosifrons* 3:1 sp. nr. *sobrina* 1:1 *setosifrons* 1:1	
Flux:		*gradata* 2:2 *sobrina* 43:3		*orthofascia* 1:1	sp. nr. *sobrina* 11:2	
Leaf:		*oahuensis* 1:1				19
Reynoldsia	x**	*gradata* 2:2			*hawaiiensis* 7:1	
Bark:		*reynoldsiae* 141:7 *sobrina* 19:2 *crucigera* 13:1	M: sp. nr. *reynoldsiae* 24:1 M: *grimshawi* 4:1			
Bark-Flux:		*gradata* 2:1 *reynoldsiae* 1:1 *sobrina* 13:1 *crucigera* 6:1			*ciliatricrus* 13:1	
Flux:		*sobrina* 43:3 *crucigera* 1:1				8
SAPINDACEAE						
Sapindus saponaria Bark: x.**		x	x	x	*engyochracea* 38:1	1
Total spp. 2		10	4	6	11	30

*n_1n_2 where n_1 = number of specimens reared and n_2 = number of collections; **= host not present on island.

TABLE 2.—Drosophila *Reared from Lobeliads*

Family	KAUAI	OAHU	LANAI/MOLOKAI	MAUI	HAWAII	Total spp.
LOBELIACEAE				*limitata* 2:2	*murphyi* 1:1	
Clermontia		*crucigera* 3:1	L: *grimshawi* 2:1	*grimshawi* 4:3		
Bark, Stem,			M: sp. nr. *planitibia* 1:1	*planitibia* 29:3	*heteroneura* 23:5	
Root, Leaf,				*disjuncta* 5:1	*silvestris* 29:4	
Flower, Fruit:			M: *cilifera* 2:1	*adiastola* 134:16	*setosimentum* 18:7	
	ornata 1:1	*neogrimshawi* 3:1	L: *adiastola* 9:1	*clavisetae* 30:4	*ochrobasis* 15:1	15
Cyanea	*villosi-*					
Bark and Stem:	*pedis* 10:1					
	crucigera 1:1					
		hemipeza 5:1		*planitibia* 2:1	*silvestris* 1:1	
	ornata 11:2			*adiastola* 4:2		
				paenehamifera 2:1		
Flower:			M: *cilifera* 2:1	*adiastola* 1:1		9
Delissea						
Stem:					*heteroneura* 3:1	1
Lobelia						
Stem:		*hemipeza* 3:1		*planitibia* 8:1		
				adiastola 4:1		3
Total spp.	3	3	L: 2, M: 2	7	4	19

TABLE 3.—Drosophila *Reared from Urticaceae*

Plant Host	KAUAI	OAHU	LANAI/MOLOKAI	MAUI	HAWAII	Total spp.
URTICACEAE						
Touchardia latifolia	*crucigera* 3:1		M: *grimshawi* 2:1			
Bark:		*touchardiae* 12:1	M: sp. nr. *touchardiae* 2:1	*peniculipedis* 21:2	sp. nr. *peniculipedis* 1:1	6
Urera kaalae		*crucigera* 3:1				
Bark:	x	*montgomeryi* 4:2	x	x	x	
		hemipeza 5:1				3
U. sandwicensis		*crucigera* 4:2	L: *grimshawi* 65:1			
Bark and Stem:		*aglaia* 1:1			*assita* 2:1	4
Total spp.	1	5	1 2	1	1	10

TABLE 4.—Drosophila *Reared from Centrospermae*

Plant Host	KAUAI	OAHU	LANAI/MOLOKAI	MAUI	HAWAII	Total spp.
AMARANTHACEAE		*crucigera* 21:4	L. *grimshawi* 10:3	*grimshawi* 5:1		
Charpentiera		*hexachaetae* 4:3		*virgulata* 75:2	*digressa* 44:2	
Stem:		*inedita* 4:2			*macrothrix* 30:1	
		tarphytrichia 3:2			*pisonia* 2:1	8
NYCTAGINACEAE	*crucigera* 2:1	*crucigera* 42:5	L: *grimshawi* 13:2	*disjuncta* 3:1		
Pisonia	*sejuncta* 1:1		M: *grimshawi* 2:1	*grimshawi* 3:2		
Stem:						
		hexachaetae 3:1		*oreas* 2:1	*macrothrix* 1:1	
		ambochila 10:3			*pisonia* 1:1	
	ocellata 1:1	*inedita* 31:4				10
Total spp.	3	5	1	4	3	15

TABLE 5.—Drosophila *Reared from Monocots*

Plant Host	KAUAI	OAHU	LANAI/MOLOKAI	MAUI	HAWAII	Total spp.
PANDANACEAE						
Freycinetia			M: *bostrycha* 12:1	*disjuncta* 7:2		
Stem:			L: *grimshawi* 9:2	*grimshawi* 5:1	*ochracea* 2:2	
					prolaticilia 1:1	
		punalua 26:3				
Fruit, Flower,		*punalua* 28:4		*balioptera* 1:1		
Leaf or Axils,				*disjuncta* 2:1		
with Frass:						7
			M: sp. nr.			
LILIACEAE			*balioptera* 1:1			
Dracaena aurea		*obatai* 29:5	M: *sodomae* 1:1		*ciliaticrus* 17:2	
Stem:	*villosipedis* 12:5	*crucigera* 70:4	L: *grimshawi* 2:1	*grimshawi* 31:2		
			M: *grimshawi* 27:2			
			L: *limitata* 3:2			
		sp. near	M: *limitata* 2:1			
		liophallus 4:1	M: *liophallus* 6:2	*liophallus* 6:2		
		psilophallus 3:2	M: *odontophallus* 54:1	*odontophallus* 4:2		
		punalua 3:2				
Leaf w. Frass:	*villosipedis* 9:1	*crucigera* 15:1				
						13
Total spp.	1	5	L: 2 M: 7	5	3	19

TABLE 6.—Drosophila *Reared from Incidental Hosts*

Plant Host	KAUAI	OAHU	LANAI/MOLOKAI	MAUI	HAWAII
BASIDIOMYCETES					
unident. mushroom		*crucigera* 6:1			
unident. jelly fungus			L: *grimshawi* 5:1		
DICKSONIACEAE, *Cibotium*					
Frond Rachis:					*setosimentum* 1:1
MARATTIACEAE, *Marattia*					*ochrobasis* 3:1
Frond Rachis:					*silvestris* 1:1
PALMAE, *Pritchardia*					
Fruit:		*crucigera* 14:1			
LAURACEAE					
Cryptocarya Fruit:		*crucigera* 65:1	x x	x	x
PIPERACEAE *Piper*					
methysticum Stem:			M: *grimshawi* 2:1		
CORYNOCARPACEAE	*crucigera* 2:1				
Corynocarpus Fruit:					
MORACEAE, *Boussonetia*		*gradata* 1:1			
papyrifera Flux:		*crucigera* 8:1			
URTICACEAE, *Pipturus*					
albidus Bark:	*crucigera* 5:1	*crucigera* 1:1			
MALVACEAE, *Hibiscus*					
Bark:					
SAPOTACEAE, *Pouteria*		*crucigera* 8:2			
(Sideroxylon) Fruit:					
PITTOSPORACEAE, *Pitto-*		*crucigera* 3:1			
sporum Sap Flux:					

Table 6.—continued

Plant Host	KAUAI	OAHU	LANAI/MOLOKAI	MAUI	HAWAII	Total spp.
LEGUMINOSAE, *Erythrina*		*crucigera* 2:1				
Bark:		*crucigera* 1:1				
Strongylodon						
Pod of Fruit:						
THYMELEACEAE, *Wikstroemia* Bark:		*crucigera* 8:1			*pullipes* 30:1	
AQUIFOLIACEAE, *Ilex*		*grimshawi* 5:3				
Bark:						
Bark-Flux:		*crucigera* 3:2				
EUPHORBIACEAE, *Euphorbia*		*gradata* 3:2				
Bark:	*villosipedis* 14:1	*crucigera* 3:1				
Aleurites Fruit:		*crucigera* 4:2				
SAPINDACEAE, *Alectryon*						
(in part) *Fruits*		*crucigera* 1:1			x	
RUTACEAE, *Pelea* Leaf:					*murphyi* 1:1	
APOCYNACEAE, *Pteralyxia*						
Fruit:		*crucigera* 14:1	x x	x	x	
SOLANACEAE, *Solanum*						
sodomeum Fruit:				*grimshawi* 1:1		
COMPOSITAE, *Dubautia*						
plantaginea Bark:		*crucigera* 14:1				
21 families. Total spp.	2	3	L: 1 M: 1	1	5	9

TABLE 7.—Drosophila *Reared from Sap Exudates*

Plant Host	KAUAI	OAHU	LANAI/MOLOKAI	MAUI	HAWAII	Total spp.
MYRSINACEAE						
Myrsine					*hawaiiensis* 2:2	
Sap Flux:		*crucigera* 1:1				
Leaf:					*ochrobasis* 1:1	3
LEGUMINOSAE		*turbata* 79:5		*recticilia* 41:1	*hawaiiensis* 15:3	
Acacia koa	*musaphilia* 35:1	*gradata* 2:1			*silvarentis* 22:1	
Sap Flux:		*crucigera* 14:3			*silvestris* 1:1	8
MYRTACEAE	*picticornis* 11:2					
Metrosideros						
Honeydew and	*picticornis* 6:2					
Sap Flux:						1
SAPINDACEAE (pars)		*flexipes* 8:2				
Sapindus		*paucicilia* 7:2	x	x	x	
oahuensis						
Sap Flux:						2
OLEACEAE					*silvarentis* 3:1	
Osmanthus		*gradata* 2:1			*hawaiiensis* 6:1	
Sap Flux:						
MYOPORACEAE					*hawaiiensis* 4:2	
Myoporum				*gymnobasis* 3:2	*silvarentis* 550:46	
Sap Flux:						
Soil wet						
with Sap:					*heedi* 214:7	4
Total spp.:	3	5	—	2	5	14

TABLE 8.—*Summary of Host Plant Groupings and Associated Cytological Groups of* Drosophila

Host Plant Group	Specimens reared	Collections	No. species reared	Cytological subgroups hosted (Principle ones capitalized)
7. SAP EXUDATES of *Acacia, Myoporum, Sapindus, Osmanthus, Myrsine* & *Metrosideros*	1027	88	14	I-2b, HAWAIIENSIS IV, *punalua* (*paucicilia* only) II, *planitibia* (*picticornis* only)
6. INCIDENTAL HOSTS: 30 native and 6 exotic species	229	36	9	I, GRIMSHAWI I-2b, *hawaiiensis* (*gradata* only)
5. MONOCOTS: *Freycinetia, Dracaena*	392	58	19	IV-b, punalua I-4b-3i, *odontophallus* I-5a, (*limitata, ochracea*)
4. PARENCHYMATOUS STEMS of *Charpentiera* and *Pisonia* (Centrospermae)	313	46	15	I-4b, *glabriapex;* I-std. I-5a, (*sejuncta* only) IV, (*ocellata* only)
3. FIBROUS BARK or LAYERED WOOD of *Touchardia* and *Urera* (Urticaceae)	125	16	10	I, *grimshawi;* 14b GLABRIAPEX III-4p, ADIASTOLA II, *planitibia* (*hemipeza* only)
2. LOBELIADS: *Clermontia, Cyanea, Lobelia, Delissea*	368	70	19	I, *grimshawi* III, ADIASTOLA II, PLANITIBIA
1. ARALIADS: *Cheirodendron, Tetraplasandra, Reynoldsia, Sapindus saponaria*	862	100	30	I-xg, ORPHNOPEZA I, *grimshawi* II, PLANITIBIA V, PRIMAEVA
TOTALS	3316	414	80	

TABLE 9.—*Substrate Types Used by Larvae of Picture-Winged and Exotic* Drosophila

Cytological Subgroup	No. spp.	Leaf	Bark	Stem	Flower	Fruit	Fungus	Sap Exudate	Insect Frass	Fern Rachis	No. Types Used
I-2b *(hawaiiensis)*	9	..	2	2	..	..	..	9	..	..	3
I-Xg *(sobrina)*	10	2	8	2	..	..	..	4	..	..	4
I-std. & I-5a *(grimshawi)*	11	2	11	8	1	5	2	2	2	..	8
I-4b *(glabriapex)*	14	..	6	10	..	..	..	..	..	..	2
IV *(punalua)*	4	1	2	3	1	..	..	..	..	..	4
III *(adiastola)*	11	2	7	6	3	2	..	..	..	2	6
II *(planitibia)*	12	1	10	8	..	..	..	1	..	1	5
V *(primaeva)*	1	..	1	..	..	..	..	..	..	..	1
Exotic species	4	..	2	1	..	3	..	3	..	..	4
Total species per substrate type:		8	49	40	5	10	2	17	2	6	
Frequency of use:		.06	.35	.29	.03	.07	.02	.12	.02	.05	

TABLE 10.—*Host Selectivity of Picture-Winged* Drosophila

	Cytological Subgroup: I	I *(cont.)*	II	III	IV	No. spp. % Total
Polyphagous**	*grimshawi* 195:28:10*	*hawaiiensis* 32:8:5				
	crucigera 327:55:21	*gradata* 15:10:5				5
	villosipedis 58:10:5					6%
Oligophagous	*murphyi* 24:6:3	*hexachaetae* 7:4:2	*silvestris* 108:7:4	*ochrobasis* 5:3:3	*punalua* 58:10:3	
	ciliaticrus 43:5:2	*pisonia* 4:2:2	*hemipeza* 14:3:2	*setosimentum* 14:10:3		15
	disjuncta 17:5:3	*limitata* 7:5:2	*picticornis* 17:2:2			
	inedita 36:6:2	*silvarentis* 575:48:3	*heteroneura* 29:8:2			17%
Monophagous: (1 family of host of plants)	*reynoldsiae* 142:8:1	*gymnobasis* 3:2:1		*peniculipedis* 24:3:1	*prolaticilia* 1:1:1	
	sp. nr. *reynoldsiae* 24:1:1	*heedi* 214:7:1	*planitibia* 41:11:1			
	engyochracea 38:1:1	*musaphilia* 35:1:1	*nigribasis* 10:6:1	sp. nr. *touchardiae* 2:1:1	*paucicilia* 7:2:1	
	sobrina 124:8:1	*turbata* 66:5:1	*oahuensis* 68:7:1			
	sp. nr. *sobrina* 15:4:1	*recticilia* 40:1:1	*cyrtoloma* 3:2:1	*touchardiae* 12:1:1	*ocellata* 1:1:1	
	orthofascia 83:7:1	*flexipes* 8:2:1	*melanocephala* 12:2:1			
	orphnopeza 13:3:1	*ochracea* 2:2:1	*neopicta* 17:3:1	*cilifera* 4:2:1	*paucipuncta* 19:1:1	
	sproati 53:3:1	*sejuncta* 1:1:1	*substenoptera* 39:3:1	*adiastola* 156:25:1		
	atrimentum 14:1:1	*aglaia* 1:1:1	*setosifrons* 7:4:1			
	obatai 29:5:1	*virgulata* 75:2:1	sp. nr. *planitibia* 1:1	*neogrimshawi* 3:1:1	Subgroup: V	
	sodomae 1:1:1	*digressa* 44:2:1		*clavisetae* 30:4:1	*primaeva* 14:2:1	
	balioptera 1:1:1	*tarphytrichia* 3:2:1		*paenehamifera* 2:1:1		
	pullipes 30:1:1	*macrothrix* 31:2:2				62
	grimshawi 10:3:1 (Kauai & Oahu)	*odontophallus* 58:3:1		*ornata* 2:11:1		77%
	pilimana 1:1:1	*psilophallus* 3:2:1		sp. nr. *peniculi-*		
	assita 2:1:1	*liophallus* 42:4:1		*pedis* 1:1:1		
	montgomeryi 4:2:1	sp. nr. *liophallus* 4:1:1				
	ambochila 10:3:1	sp. nr. *balioptera* 1:1:1				
	oreas 2:1:1	*bostrycha* 12:1				80

* $n_1:n_2:n_3$ = specimens: collections: host families

**Oligophagous: 2-4 host families
Polyphagous: >4 host families

TABLE 11.—*List of Host Plants of Picture-Winged* Drosophila

Plant, Hawaiian Name, and Origin	*Parts Utilized*
Basidiomycetes:	
unidentified jelly fungus	
unidentified mushroom	
FILICINIEAE	
Dicksoniaceae:	
E.* *Cibotium* spp. (5) (hapuu) American?	frond rachis
Marattiaceae:	
E. *Marattia douglasii* (Presl) Baker, (pala) Indo-Pacific	frond rachis
ANGIOSPERMAE, MONOCOTYLEDONAE	
Palmae:	
E. *Pritchardia* spp. (31) (loulu)	fruit
Pandanaceae:	
E. *Freycinetia arborea* Gaud. (ieie) Indo-Pacific	stem, fruit, flower
Liliaceae:	
E. *Dracaena* spp. (3) (halapepe) Indo-Pacific	stem, bark, leaf
ANGIOSPERMAE, DICOTYLEDONAE	
Lauraceae:	
E. *Cryptocarya oahuensis* (Degener) Fosberg (holio)	fruit husk
Piperaceae:	
P. *Piper methysticum* Forst. f. (awa)	stem
Corynocarpaceae:	
X. *Corynocarpus laevigata* (Forst. (N. Zea. laurel)	fruit
Moraceae:	
P. *Broussonetia papyrifera* (L.) Ven. (wauke)	sap flux
Urticaceae:	
E. *Pipturus albidus* (H. + A.) Gray (mamaki)	bark
E.G. *Touchardia latifolia* Gaud. (olona) Indo-Pacific?	bark
E. *Urera kaalae* Wawra, American	stem
E. *Urera sandwicensis* Wedd. (opuhe) American	stem
Nyctaginaceae:	
I. (2) E. (1) *Pisonia* spp. (3) (papala-kepau) Indo-Pacific and Austral	stem
Amaranthaceae:	
E. *Charpentiera* spp. (5) (papala) Austral	stem
Malvaceae:	
E. *Hibiscus arnottianus* (6) Gray (kokio keokeo)	bark
Sapotaceae:	
E. *Pouteria* (includes *Sideroxylon*) spp. (5) (alaa)	fruit
Myrsinaceae:	
E. *Myrsine lessertiana* A. DC. (kolea) Pantropic	sap flux

* The abbreviation E. signifies endemic (native only to Hawaii); E.G. signifies that the genus is endemic; I. signifies indigenous (native to Hawaii and elsewhere); P. signifies Polynesians introduced the plant before 1778, Capt. Cook's arrival; X. signifies exotic introduction after 1778. If the specific name was not determined, the approximate number of species known for the genus in Hawaii is given in parentheses after "spp.". Common names are listed when available (Porter, 1972). Regional affinities are taken from Fosberg (*in* Zimmerman, 1948) and are given for the important genera. The parts of the plant which are used as substrate for *Drosophila* larvae when in a decomposing state are listed in the right-hand column.

Pittosporaceae:
E. *Pittosporum* spp. (12) (hoawa) — sap flux

Leguminosae:
E. *Acacia koa* Gray (koa) Indo-Pacific — sap flux
X. *Erythrina variegata* (wiliwili haole) — bark
I. *Strongylodon lucidus* (Forst. f.) Seem. (nuku-iiwi)

Thymelaeaceae:
E. *Wikstroemia* spp. (20) (akia) Indo-Pacific — bark

Myrtaceae:
E. *Metrosideros collina* subsp. *polymorpha* (Gaud.) Rock (ohia) Austral — honeydew-sap flux

Aquifoliaceae:
E. *Ilex anomala* f. *sandwicensis* Endl. (kawau) Austral — bark

Euphorbiaceae:
E. *Euphorbia* spp. (14) (akoko) Indo-Pacific — bark
E. *Euphorbia haeleeleanum* Herbst — bark
P. *Aleurites moluccana* (L.) Willd. (kukui) — fruit

Sapindaceae:
E. *Alectryon macrococcus* Radlk. (mahoe) — fruit
E. *Sapindus oahuensis* Hillebr. (kaulu) Indo-Pacific — sap flux
I. *Sapindus saponaria* f. *inaequalis* (A. DC.) Radlk. (manele) American? — bark

Rutaceae:
E. *Pelea* spp. (68), (alani) Indo-Pacific — bark

Araliaceae:
E. *Cheirodendron* spp. (6), Austral — bark
E. *Cheirodendron platyphyllum* (H.&A.) Seem. (lapalapa)
E. *Cheirodendron trigynum* (Gaud.) Heller (olapa) — bark
E. *Tetraplasandra* spp. (4-20), (includes *Pterotropia*) (ohe) — affinity obscure — bark, flux, leaf
E. *Tetraplasandra hawaiiensis* Gray (ohe) — bark, sap flux, bark-flux
E. *Tetraplasandra kaalae*, Hillebr. (ohe) — bark, sap flux
E. *Tetraplasandra kahanana* Sherff (ohe) — bark
E. *Tetraplasandra kauaiensis* (H. Mann) Sherff (ohe) — bark
E. *Tetraplasandra meiandra* (Hillebr.) Harms (ohe) — bark
E. *Reynoldsia sandwicensis* Gray (ohe-o-kai) Austral — bark, bark-flux

Apocynaceae:
E.G. *Pteralyxia macrocarpa* (Hillebr.) K. Sch. (kaulu) — fruit

Solanaceae:
X. *Solanum sodomeum* L. (sodom apple) — fruit

Oleaceae:
E. *Osmanthus sandwicensis* (Gray) Knobl. (olopua) Indo-Pacific — sap flux

Myoporaceae:
E. *Myoporum sandwicense* (A. DC.) Gray (naio) Indo-Pacific — sap flux

Lobeliaceae:
E.G. *Clermontia* spp. (27) (ohawai, haha) Austral — fruit, leaf, bark of stem and root, stem
E.G. *Cyanea* spp. (60) (oha, haha) — stem, bark, flower
E.G. *Cyanea angustifolia* (Cham.) Hillebr. — stem
E.G. *Delissea undulata* Gaud. (haha) — stem
E. *Lobelia* spp. (12) (opelu) obscure
E. *Lobelia grayanum* E. Wimm. — stem
E. *Lobelia yuccoides* Hillebr. (panaunau) — stem

Compositae:
E.G. *Dubautia plantaginea* Gaud. (naenae) — bark

Appendix 1—Rearing Records

Sec. A: Hawaiian Picture-Winged Drosophila *Rearing Records Listing Collection Code, Locality, Date, Substrate, Breeding Site and Specimens Obtained.*

adiastola Hardy. Waikamoi, E. Maui, 4000 ft Feb.-Nov. 1966-71 *Clermontia* stem, 33 ♂, 25 ♀ reared from 8 collections and 1 collection (Q52) [1] of 6 specimens; stem tips and leaves, 12 ♂, 12 ♀ (G41); aerial tap root, 1 ♂, 2 ♀ (G39); leaves, 3 and 3 (G5); fruit, 1 ♂, 1 ♀ (J33) and another collection 2.[2] Kipahulu Valley, E. Maui, 2500 ft and 3100 ft, Aug. 19-67 *Clermontia* stem, 1 ♂, 2 ♀.[2]

P91 Manawainui, Kaupo, E. Maui, 4800 ft Apr. 18-71 *Clermontia* stems, 9.

R33 Waihoi Valley, E. Maui, 2200 ft July 18-72 *Clermontia* bark, 56.

P84 Hanaula, W. Maui, 3200 ft Apr. 13-71 *Clermontia* stems, 4.

Puu Kukui, W. Maui Aug.-64 *Cyanea* fruit, 3.[2]

K27 Waikamoi, E. Maui, 4000 ft July 30-67 *Cyanea* petioles and flower 1 ♂ (*1).

R10$_{\alpha}$ and β Hanaula, W. Maui, 4100 ft Apr. 28-72 *Cyanea* sp. stems, 16 and 3 .

P84 Hanaula, W. Maui, 3200 ft Apr. 13-71 *Lobelia grayanum* stems, 4.

R91 NW Lanaihale, Lanai, 2400 ft Mar. 11-73 *Clermontia* bark, 9.

aglaia Hardy Kaluaa, Puu Hapapa, W. Oahu, 1800 ft Nov. 21-71 *Urera sandwicensis* bark, 1 ♀.

ambochila Hardy and Kaneshiro. P49 and Q12 Ekahanui Gulch, Kaua, W. Oahu, 2200 ft Aug. 4-70 and Oct. 10-71 *Pisonia* stems 1 ♂, 2 ♂, 1 ♀; Aug. 30-72, 5 ♂, 1 ♀.

assita Hardy and Kaneshiro. R4 crater near Moanuiahea, Hawaii Apr. 4-72 *Urera* stem, 2 ♂.

atrimentum Hardy and Kaneshiro. P42 E. Makaleha, W. Oahu, 2300 ft Jul. 19-70 *Tetraplasandra kaalae* bark, 14.

Halawa, E. Oahu June 20-71 *Tetraplasandra* bark, 9.

balioptera Hardy. Q25 Kawaipapa Gulch, Hana, Maui, 1100 ft Dec. 14-71 *Freycinetia* leaf axils, 1.

bostrycha Hardy. R84 E. Ohia Gulch, E. Molokai 2000 ft Jan. 24-73 *Freycinetia* bark, 2.

ciliaticrus Hardy. P50 Pololu Valley, Hawaii, 1000 ft Aug. 11-70 *Dracaena* bark, 3 ♂, 3 ♀.

Q6 Puuwaawaa, Hawaii, 3600 ft Aug. 1-71 *Dracaena* stem, 11.

Q91 Poliokeawe Pali, Puna, Hawaii, 2000 ft Feb. 29-72 *Reynoldsia* stem, 1.

Q91 Kalapana, Puna, Hawaii, 100 ft Mar. 1-72 *Reynoldsia* rotting bark with sap flux, 1 ♂, 2 ♀.

R13 Fern Forest Estates, Puna, Hawaii, 3000 ft May 7-72 *Tetraplasandra hawaiiensis* stems, 1 ♂, 2 ♀.

cilifera Hardy and Kaneshiro. Kawela Intake, E. Molokai, 3600 ft Nov. 17-64 *Cyanea* sp. flowers, 2.[2]

K86 Halawa Valley, E. Molokai, 1600 ft Nov. 9-67 *Clermontia* stems, 1 ♂ 1 ♀ (in Heed, 1968 'Halauoa' is a misspelling).

clavisetae Hardy. L7 Kipahulu, E. Maui, 4300 ft Aug. 16-67 *Clermontia* stems, 1 and 1 ♂.[2]

Waikamoi, E. Maui, 4000 ft Feb.-Nov. 66-69 *Clermontia* sp. stems, 13 ♂, 15 ♀ from 8 collections.[2]

crucigera Grimshaw. J7 Halemanu, Kauai July 20-66 *Corynocarpus laevigata* fruit, 1 ♂, 1 ♀.[2]

L45 Mt. Kualapa, Kauai, 1400 ft Mar. 28-68 *Pisonia* bark, 2.

P59 Haupu, Nawiliwili, Kauai, 1800 ft Aug. 30-70 *Cyanea* stem, 1, *Pipturus* bark, 5; *Touchardia*, 3.

Kukuiala Valley, W. Oahu Sept. 16-33 *Alectryon macrococcus* fruits, 1 (Swezey, 1952).

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[1] Collection codes with a letter and numerals are given for ease of reference to laboratory records and cultures.

[2] Heed (1968).

P74 Waianae-Makaha Ridge, W. Oahu, 2600 ft Mar. 14-71 *Ilex* bark, 2; *Pittosporum* sap flux, 2.

P68 Ohikilolo Ridge, Makua, W. Oahu, 1700 ft Feb. 10-71 *Dubautia plantaginea* bark, 9.

0.7 mi. NW Puu Pane, W. Oahu, 1800 ft Feb.-Sept. 70-71, P31, *Pteralyxia* fruit, 14; *Urera sandwicensis* bark, 2; and P63, stem, 8; P10 *Charpentiera* stem, 5, *Dracaena* leaves, 15 and P73 bark, 24.

Mokuleia, W. Oahu, 2100 ft Feb.-May, 70-71, *Charpentiera* stem, 2 (P9) and 7 (P76); P77 *Pisonia* stem 4, *Euphorbia* bark, 3; P94, *Dracaena* stem, 29; P9 *Hibiscus arnottianus* bark, 7.

E. Makaleha, W. Oahu, 2000 ft Jan.-Dec. 69-72 P65 *Reynoldsia* bark of stem tip, 13, sap flux, 1, rotting bark and sap flux at termite galleries, 6; P2 *Pisonia* leaf, 1 and M83 stem, 11; P47 *Dracaena* stem, 8; Q83 *Acacia koa* sap flux, 1; P48 *Tetraplasandra kaalae* bark, 10.

Q12 Puu Kaua, W. Oahu, 2200 ft Oct. 10-71 *Ilex* bark, 1, *Myrsine lessertiana* flux, 1, *Urera kaalae* bark, 3.

Mauna Kapu, W. Oahu May 4-66 *Aleurites* fruit, 2 ♂, 1 ♀.[2]

J32 Palikea, Oahu Oct. 20-66 *Broussonetia* slime flux 5 ♂, 3 ♀;[2] P22 *Acacia koa* sap flux, 6.

P23 Kaluaa Gulch, Puu Hapapa, W. Oahu, 2100 ft Feb.-Apr. 70-72 *Tetraplasandra kaalae* bark, 5, *Urera sandwicensis* stem, 2, *Pisonia* stem, 12; P71 *Charpentiera* stem, 7, *Pipturus* bark, 1, *Strongylodon lucidus* pod, 8; P5 *Pouteria* fruit, 3; Q87 *Cryptocarya oahuensis* fruit, 65.

Pupukea, Oahu Dec. 30-63 *Freycinetia* terminal shoot with frass, 1 ♀ (Carson, 1966).

P28 Puu Manamana, Kahana, Oahu, 2000 ft May 31-70 *Tetraplasandra kahanana* bark, 3.

Q42 Castle Trail, Oahu, 2000 ft Oct. 8-71 *Clermontia* bark, 3; P12 Mar. 15-70 *Pritchardia* sp. fruit, 14.

P30 Kawaiiki, Oahu, 1300 ft July 9-70 *Dracaena* stem, 9.

P30 Opaeula, Oahu, 1200 ft July 6-70 *Pisonia* stem, 7.

Tantalus, Oahu, 1800 ft Feb. 7-70 P3 *Pisonia* stem, 14, June 18-64 *Acacia koa* slime flux, 1 (Carson, 1966), Oct. 9-63 mushroom, 6 (Carson, 1966); Jan. 10-70 M93 *Hibiscus arnottianus* bark, 1 ♂.

Lyon Arboretum, Manoa, Oahu, 400 ft Dec. 15-71 *Erythrina* bark, 1.

K37 Pia Gulch, Niu, Oahu Aug. 17-67 *Aleurites* fruits, 1 ♂.[2]

cyrtoloma Hardy. Waikamoi Flume, E. Maui, 4000 ft Aug. 10-69 *Cheirodendron trigynum* bark, 1.

P91 Manawainui, Kaupo, E. Maui, 4800 ft Apr. 21-71 *Tetraplasandra meiandra* bark, 1 ♂, 1 ♀.

digressa Hardy and Kaneshiro. Q49 Olaa Forest Reserve, Hawaii, 3600 ft Sept. 28-71 *Charpentiera* stem, 3.

Q65 Moanuiahea, Hualalai, 3800 ft Jan. 17-72 *Charpentiera* stem, 41.

disjuncta Hardy. P92 Makapipi Stream, E. Maui, 1200 ft Apr. 21-71 *Pisonia* stem, 3.

Q25 Kawaipapa, Hana, E. Maui, 1100 ft Dec. 14-71 *Freycinetia* bark, 1.

R33 Waihoi, E. Maui, 2300 ft July 13-72 *Freycinetia* fruit, 2 and stem, 6; *Clermontia* bark, 5.

engyochracea Hardy. Q91 Kipuka ki, Kilauea, Hawaii, 4000 ft Feb. 28-72 *Sapindus saponaria* bark, 38.

flexipes Hardy and Kaneshiro. P10 07. mi. NW Puu Pane, W. Oahu, 1800 ft Feb. 28-70 *Sapindus oahuensis* sap flux, 3.

P47 E. Makaleha Valley, Oahu, 1600 ft July 28-70 *Sapindus oahuensis* sap flux, 3 ♂, 2 ♀.

gradata Hardy and Kaneshiro. K20 Palikea, W. Oahu, 2800 ft July 19-67 *Broussonetia papyrifera* slime flux, 1 ♀.[2]

P2 E. Makaleha, W. Oahu, 2200 ft Feb. 8-70 *Tetraplasandra kaalae* sap flux, 1 ♂.

P46 Puu Pane, Kaala, W. Oahu, 2000 ft July 25-70, *Ilex anomala* rotting bark with

sap flux at termite gallery, 1 ♂; Mar. 7-71 P73 *Tetraplasandra kaalae* sap flux, 1 ♂; bark, 1.

P74 Makaha, W. Oahu, 1800 ft Mar. 14-71 *Osmanthus sandwicensis* sap flux, 1 ♂, 1 ♀.

P65 E. Makaleha, W. Oahu, 2000 ft Jan. 30-71 *Reynoldsia* rotting bark with sap flux at termite galleries, 2.

P66 Kului Gulch, E. Oahu, 1200 ft Jan. 31-71 *Reynoldsia sandwicensis* stems, 2 ♂, 3 ♀.

P77 Mokuleia, W. Oahu, 2300 ft Mar. 28-71 *Acacia koa* sap flux, 1 (identified by chromosomal analysis by H.L.C.).

Q12 Ekahanui, Puu Kaua, W. Oahu Oct. 12-71 *Acacia koa* sap flux, 1 (identified by chromosomal analysis by H.L.C.).

grimshawi Oidenberg. J78 Lanaihale, Lanai, 1500 ft Apr. 29-67 "jelly-fungus" on *Psidium* stem, 1 ♂, 4 ♀.[2] Q2 2800 ft June 7-71 *Tetraplasandra* bark, 1.

J99 Auwahi, E. Maui, 3000 ft June 30-67 *Solanum sodomeum* fruit, 1 ♂.[2]

L9 Kipahulu, Maui, 2500 ft Aug. 20-67 *Clermontia* stem, 1 ♂[2]

Piiholo, E. Maui, 1700 ft Oct. 25-69 *Dracaena* stems, 1 ♂.

P83 Hanaula, W. Maui, 2800 ft Apr. 12-71 *Charpentiera* wood, 5.

P91 Manawainui, Kaupo, E. Maui, 4800 ft Apr. 21-71 *Clermontia* bark, 2.

P21 Kaupo Gap, E. Maui, 4800 ft Apr. 21-71 *Pisonia* stems, 2.

Q1 Awehi, Lanaihale, Lanai, 2600 ft June 4-71 *Clermontia* stems, 5.

P85 Hanaula, W. Maui, 3400 ft Apr. 13-71 *Tetraplasandra kauaiensis* bark, 2.

Hanaula, W. Maui, 2300 ft July 15-71 *Dracaena* stems, 30.

Q20 Kaiholena Valley, Lanai, 2500 ft Nov. 11-71 *Freycinetia* bark, 4, *Pisonia* stem, 6, and (Q2) 7, *Charpentiera* stem, 4, *Urera sandwicensis* stem, 65, *Dracaena* stem, 2.

Q25 Kawaipapa, Hana, E. Maui, 1100 ft Dec. 14-71 *Freycinetia* leaf clusters, 1, bark, 5, *Clermontia* stems, 1.

Q81 Kawela, E. Molokai, 2900 ft Feb. 11-72 *Dracaena* stems, 12, *Freycinetia* bark, 5, *Charpentiera* stem, 1, *Pisonia* stem, 3, (Q7 July 14-71), 1.

Q85 Makakupaia, E. Molokai, 2100 ft Feb. 22-72 *Dracaena,* 15; *Reynoldsia* bark of stem, 4.

Q86 Mapulehu, E. Molokai, 1000 ft Feb. 13-72 *Piper methysticum* stems, 2, *Touchardia* bark, 2.

Halawa, Oahu Oct. 29-72 *Wikstroemia* bark, 2; Tantalus, Oahu Feb. 4-73, *Wikstroemia* bark, 1; Kahili, Kauai, Mar. 24-73 *Wikstroemia* bark, 2.

gymnobasis Hardy and Kaneshiro. R8$_{\alpha}$ and β Auwahi, E. Maui, 3500 ft Apr. 23-72 *Myoporum* sap flux, 1 ♀ and 2 ♀.

hawaiiensis Grimshaw. Q5 β Puuwaawaa, Hawaii, 4500 ft July 20-71 *Myoporum* sap flux, 1 ♂, 1 ♀; Q6 Aug. 25-71 *Myrsine lessertiana* sap flux, 1 ♂.

Q91 Poliokeawe Pali, Puna, Hawaii, 2000 ft Feb. 29-72 *Reynoldsia* stem, 7.

Kipuka Puaulu, Kilauea, Hawaii, 4000 ft Apr. 22-72 *Osmanthus* sap flux, 6.

Q91α and β Kipuka ki, Hawaii, 4200 ft Feb. 27-72 *Acacia koa* sap flux, 10 and 4.

Keahou Ranch, Kilauea, Hawaii 5400 ft Feb. 20-73 *Acacia koa* flux #2, 1.

Kipuka Puaulu, Hawaii 4000 ft July 13-72 *Myrsine* sap flux, 1 ♂.

heedi Hardy and Kaneshiro. Q44 Ahumoa, Pohakuloa, Hawaii, 6100 ft Sept. 25-71 *Myoporum* sap on and in soil and ground litter, 214 from 7 collections (Kaneshiro *et al.* 1973).

hemipeza Hardy. Palehua, W. Oahu, 2400 ft Oct. 11-69 *Lobelia yuccoides* stems, 1 ♂, 2 ♀.

P27 Makaha Valley, W. Oahu, 2500 ft May 28-70 *Cyanea angustifolia* bark, 5.

P72 Ekahanui, Puu Kaua, W. Oahu, 2400 ft Feb. 28-71 *Urera kaalae* bark, 2 ♂, 4 ♀.

heteroneura Perkins. G90 Huehue, Hualalai, Hawaii, 5400 ft July 1-67 *Clermontia* stems, 1 ♂, 2 ♀.[2]

Q64 1 m. N. Moanuiahea, Hualalai, Hawaii, 3800 ft Jan. 17-72 *Delissea undulata* stems, 1 ♂, 2 ♀.

R4 Moanuiahea, Hualalai, Hawaii 3600 ft Apr. 4-72 *Clermontia* stems, 2 ♂.

Q70 Kipuka, Saddle Road, Hawaii, 4140 ft Aug. 70 and Jan. 72 *Clermontia* stems, 3 ♂, 2 ♀ and 1 ♀.

$R2_{\alpha}$ Pauahi, Hawaii, 4500 ft Apr. 3-72 *Clermontia* bark, 2 ♂, 8 ♀.

Olaa Forest, Hawaii, 3800 ft Nov. 26-72 *Cheirodendron* stem, 4.

hexachaetae Hardy. P10 0.7 mi. NW Puu Pane, W. Oahu, 1800 ft Feb. 28-70 *Charpentiera* stems, 1 ♂, 1 ♀.

P76 Mokuleia, W. Oahu, 2000 ft Mar. 21-71 *Charpentiera* stem, 1.

Q24 Wailupe, E. Oahu, 1700 ft Nov. 31-71 *Pisonia* stem, 3 and *Charpentiera* stem, 1 ♀.

inedita Hardy. M83 Makaleha, W. Oahu, 2200 ft Dec. 7-69 *Pisonia* stems, 1 ♂.

Q87 Kaluaa, Puu Hapapa, W. Oahu, 1800 ft Feb. 14-72 *Charpentiera* wood and bark, 2 ♀.

M90 Manoa Cliffs, E. Oahu Jan. 1-70 *Charpentiera*, 2 ♂.

Opaeula, Oahu, 1300 ft July 16-70 *Pisonia* wood and bark, 1 ♂, 1 ♀.

P76 Mokuleia, W. Oahu, 2000 ft Mar. 21-71 *Pisonia* stems, 6 ♀.

P24 Wailupe, E. Oahu, 1700 ft Nov. 28-71 *Pisonia* wood and bark, 10 ♂, 12 ♀ (five were scarlet-eyed mutants).

limitata Hardy and Kaneshiro. E. Kawela Gulch, E. Molokai, 2900 ft Q7 July 14-71 and Feb. 11-72 *Dracaena* stems, 1 ♀ and 2 ♀.

Q20 Kaiholena Valley, Lanai, 2500 ft Nov. 11-71 *Dracaena* stems, 2 ♀.

Q52 Waikamoi, Maui, 4000 ft Nov. 15-71 *Clermontia* stems, 1 and (Aug. 72) 1.

liophallus Hardy and Kaneshiro. P83 Manawainui Gulch, Hanaula, W. Maui, 2800 ft Apr. 12-72 *Dracaena* stems, 1.

Q7 Kawela Gulch, E. Molokai, 2900 ft July 14-71 *Dracaena* stems, 8.

Q32 Manawainui Gulch, Hanaula, W. Maui July 22-71 *Dracaena* stems, 5 (larvae identified by chromosome analysis by H.L.C.).

Q82 E. Kawela Gulch, E. Molokai, 2500 ft Feb. 11-72 *Dracaena* stems, 28.

macrothrix Hardy and Kaneshiro. Kipuka Puaulu, Hawaii, 4000 ft Jul. 29-69 *Pisonia* stems, 1.

M76 Laupahoehoe, Hawaii, 2800 ft Oct. 3-69 *Charpentiera* stem, 30.

melanocephala Hardy. R22 and R33 Waihoi Valley, E. Maui, 1900 ft June 11 and July 13-72 *Tetraplasandra meiandra* bark, 12 and 2.

montgomeryi Hardy and Kaneshiro. P72 Ekahanui, Puu Kaua, W. Oahu, 2000 ft Feb. 28-71 *Urera kaalae* stems, 1 ♂ and 2 ♂, 1 ♀ (Q12, Oct. 10-71).

murphyi Hardy and Kaneshiro. N17 Kehena, Kohala, Hawaii 4000 ft July 23-69 *Pelea* leaves, 1 ♀.[2]

Q6 Halepiula, Puuwaawaa, Hawaii 4300 ft Aug. 20-71 *Cheirodendron* bark, 7.

Q9 Puu Makaala, Kulani, Hawaii, 4000 ft July 19-71 *Tetraplasandra meiandra* bark, 1 ♀. Olaa, Hawaii, 3500 ft Nov. 28-72 *Cheirodendron* bark, 3.

Q66 Moanuiahea, Hualalai, Hawaii, 3800 ft Jan. 17-72 *Cheirodendron* bark, 6.

R2 Pauahi, Hawaii, 4500 ft Apr. 3-72 *Clermontia* bark, 1 ♂.

musaphilia Hardy. Q76 Halemanu, Kauai, 4000 ft Jan. 28-72 *Acacia koa* sap flux, 35.

neogrimshawi Hardy and Kaneshiro. Q42 Castle Trail, Oahu, 1900 ft Sept. 10-71 *Clermontia* bark, 3.

neopicta Hardy and Kaneshiro. P84 Hanaula, W. Maui, 2300 ft Apr. 13-71 *Tetraplasandra kauaiensis* stems, 14.

P91 Manawainui, Kaupo, E. Maui, 4800 ft Apr. 21-71 *Tetraplasandra meiandra* bark, 2.

Q3 Puu Kolekole, E. Molokai, 3300 ft June 9-71 *Cheirodendron trigynum* bark, 1.

nigribasis Hardy. N35 Kaala, W. Oahu, 4000 ft Jan. 28-70 *Cheirodendron platyphyllum* stems, 1 ♂.

P12 Castle Trail, Oahu, 2100 ft Mar. 15-70 *Tetraplasandra* bark, 1.

Kaala, W. Oahu, 4000 ft Oct. 15-70 *Cheirodendron platyphyllum* bark, 2.

P74 Makaha Trail, Kaala, W. Oahu, 2600 ft Mar. 14-71 *Cheirodendron* bark, 1 ♂.

Q11 Konahuanui, Oahu, 2700 ft Sept. 19-71 *Cheirodendron platyphyllum* bark, 3; *Tetraplasandra* bark, 2 ♂.

oahuensis Grimshaw. P12 Castle Trail, Oahu, 2100 ft Mar.-Apr.-70 *Tetraplasandra* bark, 1 and (P21) 3; leaves, 1.
P25 Dupont Trail, Kaala, W. Oahu, 3600 ft May 20-70 *Cheirodendron platyphyllum* bark, 1.
P28 Manamana, Kahana, E. Oahu, 2000 ft May 31-70 *Tetraplasandra kahanana* bark, 9.
P73 Puu Pane, W. Oahu, 1800 ft Mar. 7-71 *Tetraplasandra kaalae* bark, 1 ♂.
P74 Makaha Trail, Kaala, Oahu, 2600 ft Mar. 14-71 *Cheirodendron* bark, 51.
Q11 Konahuanui, Oahu, 2800 ft Oct. 19-71 *Tetraplasandra meiandra* bark, 1.

obatai Hardy and Kaneshiro. P10 Puu Pane, Kaala, W. Oahu, 1800 ft Feb. 28-70 *Dracaena* bark, 4.
P47 E. Makaleha, W. Oahu, 1700 ft July 28-70 *Dracaena* bark, 1 ♀.
P73 Puu Pane, Kaala, W. Oahu, 1900 ft Mar. 7-71 *Dracaena* stems, 9.
Q24 Wailupe, E. Oahu, 1700 ft Nov. 28-71 *Dracaena* stem, 12; Q18 Waialae Nui, E. Oahu, 1400 ft Oct. 17-71 *Dracaena* stem, 3.

ocellata Hardy and Kaneshiro. L45 Kualapa, Kauai, 1400 ft Mar. 28-68 *Pisonia* stem, 1 ♂ (Hardy and Kaneshiro, 1969).

ochracea Grimshaw. J6 Honaunau, Hawaii, 2100 ft July 20-66 *Freycinetia* stems, 1 ♂.
R13 Puna Forest Reserve, Hawaii, 3000 ft May 7-72 *Freycinetia* bark, 1.

ochrobasis Hardy and Kaneshiro. Huehue, Hualalai, Hawaii, 5500 ft June 13-66 *Myrsine* leaves (dissected from puparium), 1 ♂.[2]
Kipuka no. 9 Saddle Rd., Hawaii, 5000 ft Sept. 26-71 *Marattia douglasii* rachis, 3.
Kau Forest Reserve, Hawaii, 4500 ft June-72 *Clermontia* aerial root, 15.

odontophallus Hardy and Kaneshiro. P18 Auwahi, E. Maui, 3500 ft Apr. 4-70 *Dracaena* stems, 1 ♂, 1 ♀.
Q32 Manawainui Gulch, Hanaula, W. Maui July 22-71 *Dracaena* stems, 2 (H.L.C. identified by larval chromosome analysis).
Q81 Kawela Gulch, E. Molokai, 2900 ft Feb. 11-72 *Dracaena* stems, 54.

oreas Hardy. Q61 Puakaa, Hana, E. Maui, 1200 ft Dec. 13-71 *Pisonia* stem, 1 ♂, 1 ♀.

ornata Hardy and Kaneshiro. P60 Kanaele Bog, Kahili, Kauai, 2200 ft Sept. 2-70 *Cyanea* stems, 1.
N23 Kahili, Kauai, Aug. 12-69 *Cyanea* stem, 10.[2]

orphnopeza Hardy and Kaneshiro. P85 Hanaula, W. Maui, 3400 ft Apr. 13-71 *Tetraplasandra kauaiensis* bark, 1 ♀.
Waihoi Valley, E. Maui, 1900 ft June 11, July 15-72 *Tetraplasandra meiandra* bark 5 (R22) and 7 (R33).

orthofascia Hardy and Kaneshiro. Q20 Kaiholena Valley, Lanai 2500 ft Nov. 11-71 *Tetraplasandra hawaiiensis* bark, 32.
Q25 Kawaipapa, Hana, E. Maui, 1100 ft Dec. 14-71 *Tetraplasandra hawaiiensis* bark-flux, 23; flux, 1 ♀; stem, 1 ♀.
R22 Waihoi Valley, E. Maui, 1900 ft June 11 and July 15-72 *Tetraplasandra* meiandra bark, 3; *Tetraplasandra hawaiiensis* bark on root, 10 ♂, 12 ♀; *Cheirodendron* bark, 1.

paenehamifera Hardy and Kaneshiro. R10 Hanaula, W. Maui, 4100 ft Apr. 28-72 *Cyanea* stems, 2.

paucicilia Hardy and Kaneshiro. P10 0.7 mi. NW Puu Pane, W. Oahu, 1800 ft Feb. 28-70 *Sapindus oahuensis* sap flux, 2.
P47 E. Makaleha Valley, W. Oahu, 1600 ft July 28-70 *Sapindus oahuensis* sap flux, 5.

paucipuncta Grimshaw. Olaa Forest, Hawaii, 3800 ft Nov. 26-72 *Cheirodendron* stems, 19.

peniculipedis Hardy. P84 Pohakea, Hanaula, W. Maui, 3000 ft Apr. 13-71 *Touchardia* bark, 13.
R10 Hanaula, W. Maui, 4100 ft Apr. 28-72 *Touchardia* bark, 8.
R33 Waihoi, E. Maui July 13-72 *Touchardia* bark, 3.

picticornis Grimshaw. Kokee, Kauai, Mar. 15-65 *Metrosideros* slime flux, 1.[2]
P54 Milolii, Kauai, 1800 ft Aug. 22-70 *Metrosideros polymorpha* sap flux from *Oliarus* (Homoptera; Cixiidae) honeydew, 5.

Q76 Halemanu, Kauai, 3600 ft Jan. 28-72 *Acacia koa* sap flux, 3.
P56 Poomau, Mohihi, Kauai, 3600 ft Aug. 25-70 *Acacia koa* sap flux, 8.

pilimana Grimshaw. P25 Dupont Trail, Kaala, W. Oahu, 3600 ft May 20-70 *Cheirodendron* bark, 1 ♀.

pisonia Hardy and Kaneshiro. M95 Pololu Stream, Kohala, Hawaii, 1400 ft Jan. 13-70 *Pisonia* stem, 2 ♂ and *Charpentiera* stem, 2 ♂.

planitibia Hardy. Waikamoi, Maui, 4000 ft Feb.-Aug. 1966-67 *Clermontia* stems, 10 ♂, 13 ♀ from 5 collections[2] and 5 from Q52 (Nov. 15-71).
L7 Kipahulu, E. Maui, 4300 ft Aug. 16-67 *Clermontia* stems, 1 ♂ (*1).
P84 Pohakea, Hanaula, W. Maui, 3200 ft Apr. 13-71 *Lobelia grayanum* stems, 8.
P91 Manawainui, Kaupo, E. Maui, 4800 ft Apr. 21-71 *Clermontia* stems, 1.
$R10_{\alpha}$ Hanaula, W. Maui, 4100 ft Apr. 28-72 *Cyanea* stems, 2.

primaeva Hardy and Kaneshiro. P60 Kahili, Kauai, 2700 ft Sept. 2-72 *Cheirodendron* bark, 2 ♂, 3 ♀; *Tetraplasandra* bark, 5 ♂, 4 ♀.

prolaticilia Hardy. R13 Puna Forest Reserve, Hawaii, 1600 ft May 7-72 *Freycinetia* bark, 1.

psilophallus Hardy and Kaneshiro. P30 Opaeula, Oahu, 1200 ft June 8-70 *Dracaena* bark, 1.
Kawaiiki, Oahu, 1300 ft June 8-70 *Dracaena* stems, 2.

pullipes Hardy and Kaneshiro. R13 Kalapana, Puna, Hawaii, 1600 ft May 7-72 *Wikstroemia* bark, 30.

punalua Bryan. K5 Mauna Kapu, W. Oahu July 11-67 *Freycinetia* leaf (with eggs deposited along vein) 6 ♂, 6 ♀.[2]
Tantalus Trail, E. Oahu Oct. 22-63 *Freycinetia* flower, 7; Sept. 11-63 *Freycinetia* leaf axils with *Catamempsis* (Lep.) frass, 6.[2]
Palikea, W. Oahu, 2400 ft Oct. 11-69 *Freycinetia* leaf axils, 3.
Kaala, W. Oahu, 4000 ft Jan. 19-70 *Freycinetia* bark, 5.
P10 0.7 mi. NW Puu Pane, W. Oahu, 1800 ft Feb. 28-70 *Dracaena* bark, 2 ♂.
P30 Opaeula, Oahu, 1300 ft July 16-70 *Dracaena* stems, 1 ♀.
Q11 Konahuanui, Oahu, 2800 ft Oct. 19-71 *Tetraplasandra meiandra* bark, 1 ♀; *Freycinetia* stems, 16.
Q23 Manamana, Kahana, Oahu, 1900 ft Nov. 21-71 *Freycinetia* bark and leaf, 5.

recticilia Hardy and Kaneshiro. Q37 Kahualua, Kaupo, E. Maui, 2600 ft Aug. 15-71 *Acacia koa* sap flux, 40.

reynoldsiae Hardy and Kaneshiro. E. Makaleha, E. Oahu, 1200 ft -2300 ft Jan.-July 70-71 *Reynoldsia* bark, 41 (P42), 3 (P2), 39 (P65); bark-flux associated with termite galleries, 1.
P44 Lower Peacock Flats, W. Oahu July 21-70 *Reynoldsia* bark of stems, 28.
P73 NW Puu Pane, W. Oahu Mar. 7-71 *Reynoldsia* bark, 8.
P75 Kealia Trail, Mokuleia, W. Oahu, 300 ft Mar. 21-71 *Reynoldsia* bark, 4.
P66 Kului Gulch, E. Oahu, 1200 ft Jan. 31-70 *Reynoldsia* bark, 8.

sejuncta L45 Mt. Kualapa, Kauai, 1400 ft Mar. 28-68 *Pisonia* wood and bark, 1 ♂.

setosifrons Hardy and Kaneshiro. P50 Honokane Nui, Kohala, Hawaii, 1500 ft Aug. 10-70 *Tetraplasandra hawaiiensis* rotting bark with sap flux, 1.
N72 Papa, S. Kona, Hawaii, 2700 ft Mar. 1-73 *Tetraplasandra hawaiiensis* bark of windfall tree, 3.
Q6 Puuwaawaa, Hawaii, 4300 ft Aug. 20-71 *Cheirodendron trigynum* bark, 1.
Q66 SE Moanuiahea, Hawaii, Jan. 17-72 *Cheirodendron* bark, 2.

setosimentum Hardy and Kaneshiro. G69 Kipuka, Saddle Rd., Hawaii 2275 ft June 2-66 *Clermontia* stems, 2 ♀.[2]
G78 Holualoa, Hualalai, Hawaii, 2625 ft June 12-66 *Clermontia* leaf and fruit, 1 ♂.[2]
Awini, N. Kohala, Hawaii Aug. 2-66 *Clermontia* bark J17 (no. specimens not given)[2]
Clermontia leaves, fruits, flowers, 1 ♂ (J18).
Upper Olaa, Hawaii, 4000 ft May 28, June 20-68 *Cibotium* frond, 1 (L71); *Cheirodendron trigynum* bark of branch, 2 (L82).[2]

Q58 Kipuka, Saddle Rd., Hawaii, 4140 ft Jan. 19, Dec. 10-71 *Clermontia* stems, 1 (Q58) and 1 (Q70).

Q6 Moanuiahea, Hualalai, Hawaii, 3800 ft Apr. 4-72 *Clermontia* stems, 1 ♂ (R4) and 1 (Q66).

silvarentis Hardy and Kaneshiro. N27 Pohakuloa, Hawaii, 6000 ft Jan. 18-70 *Myoporum* sap flux, 40 specimens from 5 collections.

Puuwaawaa, Hawaii, 4500 ft July 25-70 *Myoporum* sap flux, 11 from 3 collections.

Q10 Papa, S. Kona, Hawaii Aug. 20-71 *Osmanthus*, 3.

Q48 Kilauea Forest, Hawaii Sept. 27-71 *Myoporum* sap flux, 42 (Kaneshiro et al., 1973); Mar. 7-73, 4.

Q65α and β 1 mi. N. Moanuiahea, Hualalai, Hawaii, 3800 ft Jan. 17-72 *Myoporum* sap flux, 1 and 2.

$R7_{\alpha}$ Papaloa, Kona, Hawaii, 5100 ft Apr. 6-72 *Myoporum sandwicense* sap flux, 1 ♀.

Pohakuloa, Hawaii, 6000 ft 1971-72 *Myoporum* sap flux, 449 from 33 collections (Kaneshiro et al., 1973). N51 Laupahoehoe, Hawaii, 3000 ft Feb. 13-73 *Acacia koa* sap flux, 22.

silvestris Perkins. Q58 Kipuka, Saddle Rd., Hawaii, 4140 ft Dec. 10-71 *Clermontia* bark, 2 ♂, 1 ♀.

Q88 Kipuka "no. 14", Saddle Rd., Hawaii, 5100 ft Feb. 27-72 *Cyanea* stems, 1 ♀.

N79 Kipuka "no. 14" Saddle Rd., Hawaii, 5100 ft Mar. 10-73 *Cheirodendron* bark, 4.

Q89 Kipuka "no. 9", Saddle Rd., Hawaii, 5108 ft Feb. 25-72 *Marattia douglasii* rachis, 1 ♀ (specimen undersized).

R2 Pauahi, Hawaii, 4500 ft Apr. 3-72 *Clermontia* bark, 5 ♂, 15 ♀.

R16 Kau Forest Reserve, Hawaii, 4500 ft June 12-72 *Clermontia* bark, 78.

Keahou Ranch, Kilauea, Hawaii, 5400 ft Feb. 20-73 *Acacia koa* flux #2, 1 ♂.

sobrina Hardy and Kaneshiro. P28 Manamana, Kahana, E. Oahu, 1900 ft May 31-70 *Tetraplasandra kahanana* bark, 45.

P44 Mokuleia, W. Oahu, 1200 ft July 21-70 *Reynoldsia* bark of stem, 3.

P47 E. Makaleha, W. Oahu, 1700 ft July+Jan., 70+71 *Reynoldsia* bark, 16 (P47), bark-flux, 13 (P47), sap flux, 4 (P65); *Tetraplasandra kaalae* sap flux with soil, 2.

P73 Puu Pane, Kaala, W. Oahu, 2000 ft Mar. 7-71 *Tetraplasandra kaalae* sap flux with soil, 39.

Q19 Kaunala, Pupukea, Oahu, 1500 ft Oct. 31-71 *Tetraplasandra* sap flux, 1 ♂, 1 ♀.

sodomae Hardy and Kaneshiro. Q81 E. Kawela, E. Molokai, 2900 ft Feb. 11-72 *Dracaena* stems, 1 ♀.

sproati Hardy and Kaneshiro. Q70 Saddle Rd., Kipuka, Hawaii, 4140 ft Jan. 19-72 *Cheirodendron* bark, 47.

N48 S. Kohala, Hawaii, 4000 ft Feb. 11-73 *Cheirodendron* bark, 3.

N79 Kipuka "no. 14", Saddle Rd., Hawaii, 5100 ft Mar. 10-73 *Cheirodendron* bark, 3.

substenoptera Hardy. P12 Castle Trail, Oahu, 2100 ft Mar. 15-70 *Tetraplasandra* bark, 2 ♀.

P25 Dupont Trail, Kaala, W. Oahu, 3600 ft May 20-70 *Cheirodendron platyphyllum* bark, 3 ♀.

P74 Makaha Trail, Kaala, W. Oahu, 2600 ft Mar. 14-71 *Cheirodendron* bark, 34.

tarphytrichia Hardy. P23 Kaluaa, Puu Hapapa, W. Oahu, 1800 ft Apr. 26-70 *Charpentiera* stem, 1 ♂ (P23, Apr. 26-70) and 2 (P71, Feb. 21-71).

touchardiae Hardy and Kaneshiro. P64 Pia Stream, Niu, E. Oahu, 1400 ft Jan. 23-71 *Touchardia* bark, 12 (Hardy and Kaneshiro 1972).

turbata Hardy and Kaneshiro. P23 Kaluaa, Puu Hapapa, W. Oahu, 2000 ft Apr. 26-70 *Acacia koa* sap flux, 5 ♂, 6 ♀.

Puu Pane, Kaala, W. Oahu, 1900 ft May 3-24-70 *Acacia koa* sap flux, 2 ♂, 1 ♀ (F24) and 14 (P26).

P27 Makaha, W. Oahu, 1900 ft May 31-70 *Acacia koa* sap flux, 15.

Q11 Waahila Ridge, Oahu, 1350 ft Sept. 19-71 *Acacia koa* sap flux, 36.

villosipedis Hardy. P53 Nonou, Kapaa, Kauai, 700 ft Sept. 19-70 *Dracaena* stems, 4 ♂, 7 ♀.

P54 Mahanaloa, Milolii, Kauai, 1800 ft Aug. 22-70 *Euphorbia haeleeleanum* bark of

stem, 7 ♂, 7 ♀; *Dracaena* bark, 2 ♂ and stem, 1 ♂.

P55 Honopu, Kokee, Kauai, 3600 ft Aug. 23-70 *Dracaena* bark, 3 ♂.

P56 Poomau, Mohihi, Kauai, 3700 ft Aug. 25-70 *Acacia koa* sap flux, 1; *Tetraplasandra* bark, 2.

P59 Haupu, Nawiliwili, Kauai, 1600 ft Aug. 30-70 *Cyanea* stems, 6 ♂, 4 ♀.

P60 Kanaele, Kahili, Kauai, 1800 ft Sept. 2-70 *Dracaena* stems, 4; leaf axils with Lep. frass, 9.

virgulata Hardy and Kaneshiro. P82 Makamakaole, W. Maui, 1200 ft Apr. 11-71 *Charpentiera* stem, 29.

P83 Manawainui, Hanaula, W. Maui, 2800 ft Apr. 12-71 *Charpentiera* stem, 46.

species near *reynoldsiae* Q94 Halawa, E. Molokai, 300 ft Mar. 5-72 *Reynoldsia* bark, 24.

species near *sobrina* Honokane Nui, Kohala, Hawaii Aug. 10-70 *Tetraplasandra hawaiiensis* bark-flux, 1 ♀ (P50$_\alpha$, 1500 ft), sap flux, 1 ♂ (P50β, 1200 ft).

P50λ Pololu Trail, Kohala, Hawaii, 1000 ft Aug. 11-70 *Tetraplasandra hawaiiensis* sap flux, 10.

Q10 Papa, S. Kona, Hawaii, 2000 ft Aug. 20-71 *Tetraplasandra hawaiiensis* bark, 3.

species near *balioptera* R85 Waiakuilani Gulch, E. Molokai, 3100 ft Jan. 25-73 *Freycinetia* stem, 1 ♂.

species near *touchardiae* Q86 Mapulehu, E. Molokai, 1000 ft Feb. 13-72 *Touchardia* bark, 1 ♂, 1 ♀.

species near *peniculipedis* R13 Kalapana, Puna Forest Reserve, Hawaii, 1600 ft May 7-72 *Touchardia* bark, 1 ♀.

species near *planitibia* Q84 S. Hanalilolilo, E. Molokai Feb. 12-71 *Clermontia* stem, 1.

species near *liophallus* P10 0.7 mi NW Puu Pane, W. Oahu, 1800 ft *Dracaena* bark, 4.

Sec. B. Rearing Records for D. quasianomalipes

quasianomalipes Hardy. P56 Poomau, Mohihi, Kauai 3700 ft Aug. 25-70 *Tetraplasandra* bark, 1 ♂; P59 Haupu, Nawiliwili, Kauai 2200 ft Aug. 30-70 *Cheirodendron* bark, 4 ♂, 4 ♀; Kawaikoi, Kauai 4000 ft Oct. 15-72 *Cheirodendron* bark, 1 ♂.

Sec. C. Rearing Records for Drosophilidae Exotic to Hawaii

Genus CHYMOMYZA

procnemis Williston. Puu Pane, Kaala, W. Oahu, 1800 ft *Acacia koa* broken bark with sap, 2.

Genus DETTOPSOMYIA

formosa Lamb. Kahakuloa, Maui, 300 ft Oct. 25-69 *Aleurites moluccana* fruit, 2.

Genus DROSOPHILA

carinata Grimshaw. P21 Castle Trail, Kahana, E. Oahu Apr. 11-70 *Touchardia* bark, 1.

immigrans Sturtevant. Kahakuloa, Maui, 300 ft Oct. 25-69 *Aleurites moluccana* fruit, 44.

P33 Puu Pane, Oahu, 1800 ft June 18-70 in soil with sap from *Sapindus oahuensis* flux, 7; P46 July 25-70 *Pteralyxia* fruit, 24.

Q1 Awehi Gulch, Lanai, 2600 ft June 4-70 *Clermontia* stems, 3.

Q25 Kawaipapa Gulch, Hana, Maui, 1100 ft Dec. 14-71 *Clermontia* stems, 5.

Lyon Arboretum, Manoa, Oahu, 400 ft Dec. 15-71 *Erythrina* bark, 6.

Q62 Wiliwilinui Ridge, Oahu Dec. 18-71 *Freycinetia* fruit, 12.

Q86 Mapulehu, Molokai, 1000 ft Feb. 1-72 *Piper methysticum* stems, 34.

simulans Sturtevant. Q93 Makolelau, E. Molokai, 3000 ft Mar. 4-72 *Gouldia terminalis* ex sap on broken stem, 1 ♂, 2 ♀.

COLLECTORS

Noted here are the collectors who in varying degrees have contributed to Appendix I: S. L. Montgomery, 291 collections; Kenneth Y. Kaneshiro, 26; H. L. Carson, 21; W. B. Heed, 21; Robert Iwamoto, 12; D. E. Hardy, 6; John K. Obata, 6; Charles Whittle, 4; Douglas Fujii, 4; M. R. Wheeler, 4; W. W. Steiner, 3; Mercedes Delfinado, 4; Wayne Ibara, 2; H. T. Spieth, 2; Rick Warshauer, 2; J. P. Murphy, 2; R. H. Richardson, 2; Walter Johnson, 2; Elysse Craddock, 2; Michael Kambysellis, 1; S. K. Ochikubo, 1; Barnard Ward, 1; D. S. Yoshioka, 1; Kathleen Resch, 1.

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